Changes in deep-water epibenthic megafaunal assemblages in relation to seabed slope on the Nigerian margin

Daniel O. B. Jones[1*], Charles O. Mrabure[2] and Andrew R. Gates[1]

* corresponding author

[1] SERPENT Project, National Oceanography Centre, European Way, Southampton, SO14 3ZH, UK.

[2] Total E & P Nigeria Ltd., 37 Kofo Abayomi Street, Victoria Island, Lagos, Nigeria

Abstract

Local-scale habitat heterogeneity associated with changes in slope is a ubiquitous feature of bathyal continental margins. The response of deep-sea species to high habitat heterogeneity is poorly known and slope can be used as a proxy for many important ecological variables, such as current flow, sedimentation and substratum type. This study determines how slope angle effects megafaunal species density and diversity at the Usan field, offshore Nigeria, between 740-760 m depth. This deep-water area is increasingly exploited for hydrocarbons, yet lacking in baseline biological information. Replicated remotely operated vehicle video transect surveys were carried out using industry infrastructure (through the SERPENT Project) at a representative range of slopes (1°, 3°, 11° and 29°). Twenty-four species of benthic megafaunal invertebrate were found, numerically dominated by the echinoid *Phormosoma placenta*, and nine species of fish were observed. Megafaunal invertebrate deposit feeder density decreased significantly with increasing slope (density range 0.503 - 0.081 individuals m^{-2}). Densities of megafaunal suspension feeders were very low except at the highest slope site (mean density 0.17 m^{-2}). Overall species richness was greater on steeper slopes, although the richness of deposit feeders was not affected. Reduced labile organic matter in sediments on steeper slopes

likely reduced deposit feeder densities, but increased current flow at higher slopes allowed both increased richness and density of suspension feeders.

Keywords:
Deep-sea; slope; habitat heterogeneity; landscape; Phormosoma placenta; Gulf of Guinea, Nigeria; video

1. Introduction

Habitat heterogeneity at local scales is a ubiquitous feature of bathyal continental margins and exerts a fundamental influence on the diversity and structure of benthic communities (Levin and Dayton, 2009). The 'habitat heterogeneity hypothesis' is one of the cornerstones of ecology (e.g. MacArthur and Wilson, 1967; Simpson, 1949). It assumes that structurally complex habitats may provide more niches and diverse ways of exploiting the environmental resources and thus increase species diversity (Tews *et al.*, 2004). Characterisation of the seabed in terms of terrain parameters, such as slope and aspect, is a potentially valuable tool for classifying the structural complexity of the seabed and delineating regions of seabed that may support particular fauna and therefore provide a distinct habitat (Wilson *et al.*, 2007). These techniques, broadly classified as habitat mapping, have been successful in shallow waters (Lundblad *et al.*, 2006) and are receiving increased attention in deep water (Jones and Brewer, 2012; Wilson *et al.*, 2007). Slope is a commonly used and important parameter in these analyses, but direct assessment of changes in deep-water assemblages in relation to seabed slope have not (to the author's knowledge) been assessed quantitatively. Flat areas tend to exhibit different seabed facies and support communities that are different to those inhabiting steeply sloping areas (Lundblad *et al.*, 2006; Schlacher *et al.*, 2007). Slope, as with depth, is not a direct environmental factor that controls biological communities; rather it is a useful proxy for correlated but unmeasured factors. In the case of slope, these environmental factors range across the scale of investigation but include a complex of environmental variables, primarily habitat heterogeneity (Schaff *et al.*, 1992), local current flow (Noble and Mullineaux, 1989; Palardy and Witman, 2011), sedimentation, substratum type, food availability and colonisation (Butman, 1990; Butman *et al.*, 1994; Gage, 1997). Shallow water

research suggests that these factors may lead to increases in density (Sebens, 1985), higher diversity (Palardy and Witman, 2011), elevated growth rates and changes in species distribution (Leichter and Witman, 1997) as well as functional changes in benthic communities, for example favouring suspension feeding over deposit feeding organisms (Jumars and Nowell, 1984). It is important to assess the role of slope-related factors in driving the structure of deep-water benthic faunal assemblages (Levin *et al.*, 2001; Tyler, 1995), particularly in areas of high habitat complexity such as canyons (De Leo *et al.*, 2010; Rowe *et al.*, 1982) and seamounts (Clark *et al.*, 2010; Genin *et al.*, 1986).

By combining spatially-accurate quantitative seabed imaging techniques with high-resolution acoustic data on submarine topography and sediment properties fine-scale patterns in megafaunal biology can be linked to the broad-scale patterns in habitat type and subsea landscape (Baguley *et al.*, 2006; Wilson *et al.*, 2007). Given the sheer size and difficulties of accessing the deep-sea environment, accurate extrapolation of fine-scale observations using information on the important physical controls for faunal distribution is vital to describe the important broad-scale patterns in benthic biology (Sanchez *et al.*, 2008; Williams *et al.*, 2010). Characterising variation in biodiversity and biological assemblage structure in response to specific terrain parameters, such as slope, are important to help understand the underlying mechanisms behind these patterns.

The megabenthic communities of the offshore waters of the Gulf of Guinea region are poorly known (Le Loeuff, 1993; Le Loeuff and von Cosel, 1998; Lebrato and Jones, 2009) compared to the Canary region to the north (Duineveld *et al.*, 1993a; Duineveld *et al.*, 1993b; Henriques *et al.*, 2002; Jones and Brewer, 2012; Keller and Pasternak, 2002; Merrett and Domanski, 1985; Merrett and Marshall, 1981). The Benguela region to the south of the Gulf of Guinea has also received some attention, particularly on the shelf and slope (Roeleveld *et al.*, 1992; Roy *et al.*, 2007; Uriz, 1988) as well as the abyss (Kroncke and Turkay, 2003; Levin and Gooday, 2001; Saiz-Salinas, 2007; Thandar, 1999; Vinogradova *et al.*, 1990; Zibrowius and Gili, 1990). The Gulf of Guinea region is heavily exploited for natural resources, primarily hydrocarbon resources (Zabanbark, 2002) and fish (FAO Fishery Committee for the Eastern Central Atlantic, 1991) and is subject to high levels of anthropogenic impact

from pollution, mostly of terrestrial origin (Scheren *et al.*, 2002). The limited environmental information is mostly collected by oil and gas companies and not available in the scientific literature. However, it is crucial that baseline quantitative environmental information is available for successful management of this increasingly exploited ecosystem.

This paper provides the first description of deep-water megabenthic assemblages at a deep-water Nigerian site. Quantitative remotely operated vehicle (ROV) imaging allowed the effect of various seabed slopes on assemblage density, composition and diversity to be assessed. Specifically, the following hypotheses were tested: 1) increases in environmental heterogeneity associated with slope will increase megafaunal species richness, 2) increased slope will favour suspension feeding lifestyles at the expense of deposit feeding and hence change the relative abundances of these functional groups and 3) the combination of these effects will lead to differences in megafaunal assemblage structure between habitats with biologically significant variation in environmental conditions resulting from changes in slope.

2. Methods

2.1. Study Site

This study focuses on a knoll at the west of the Usan field (within Nigerian offshore oil prospecting license block 222), an area that will be developed for hydrocarbon production, located on the Nigerian continental margin in the Gulf of Guinea. Environmental baseline surveys (Total E. & P. Nigeria Ltd., 2007) in the main Usan field (centred 03° 31.800' N 007° 26.400' E; slope < 1°) collected boxcore samples of seabed sediments. The silty clay sediment was comprised of silt (50.1 ± 1.1 %; mean ± standard deviation), clay (34.9 ± 2.0%) and sand (15.1 ± 1.0 %), with an organic content of 5.8 ± 1.3% and a total organic carbon content of 3.3± 0.7 %. Sediments contained abundant material or terrigenous origin (e.g. seeds, pollen, plant material). Sediments supported a macrofaunal (>0.5 mm) assemblage with low density (69 ± 53 individuals m^{-2}) and diversity (57 species). The macrofauna was dominated by molluscs (38.6%), arthropods (22.0%), protozoans (17.6%) and annelids (16.3%),

with the remainder comprised of echinoderms, cnidarians, poriferans and hemichordates (Total E. & P. Nigeria Ltd., 2007).

Shipboard measurements of seawater collected near the seabed at Usan had dissolved oxygen levels (mean = 5.84 mg L^{-1} [54.7 % saturation], range = 4.41 [40.8 %] to 9.54 [88.4 %] mg L^{-1}) that were not hypoxic (dissolved oxygen is < 0.7 mg L^{-1} (Helly and Levin, 2004)). *In situ* physical measurements of the near-bottom seawater (at 750 ± 10 m water depth) made during this study showed low temperatures (5.32 ± 0.07 °C; mean ± standard deviation) and consistent salinities (34.76 ± 0.01).

2.2. Survey Design

Four habitats, each with different slope conditions (1°, 3°, 11° and 29°), were assessed at Usan (Figure 1) through the SERPENT project (Jones, 2009). The slope conditions were labelled 1°, 3°, 11° and 29°. For each slope condition an area was chosen within the Usan field using detailed bathymetric charts (Figure 1) that fulfilled the following criteria: constant slope, a depth between 740 and 760 m and a distance of at least 1 km from any drilling activity to ensure no effect of disturbance (Jones *et al.*, 2006). Three replicate remotely operated vehicle (ROV) video transects (200 m length) were performed at random locations within each slope condition (S1). Survey start points and survey direction were identified using a random number generator in Microsoft Excel. Transects were examined by plotting them onto the chart. Any transect that extended beyond the boundaries of identified areas was discarded and another generated using the same method. In the area of highest slope headings were constrained between 350 to 360°, 0 to 10° and 170 to 190° to maintain the depth range of transects but otherwise were random. Each transect was regarded as a sampling unit (i.e. all organism densities were totalled for each 200 m transect) and used in all subsequent analysis. Three replicate transects at four slope levels resulted in a total of 12 sampling stations. All positional information was recorded in Universal Transverse Mercator (UTM) zone 32 N based on the World Geodetic Society 1984 datum.

2.3. Data collection

Data were collected using an Oceaneering Millennium ROV equipped with a colour video camera (Insite Pacific Pegasus), sonar and ultra-short baseline navigation transponder. Cameras were mounted on a pan and tilt unit at the front of the ROV, which enabled oblique video to be taken. Before each transect the video was zoomed out to maximum extent and the camera was set to its most vertical angle (30° below the horizontal).

In every transect the ROV was run in a straight line, on a set bearing and at a constant speed (~0.3 m s^{-1}). Vehicle altitude (distance from seabed to the base of the ROV) was kept constant at 1 m, which equated to a 143 cm camera altitude (from the centre of the camera). Transect width (mean of 1.72 m; max variation ± 0.2 m) was calculated from the camera acceptance angles (Jones *et al.*, 2006). The camera horizontal acceptance angle (at full wide angle) was 55° and the vertical acceptance angle 43°. Transect width was also verified by passing over objects of known size on the seafloor. The optical resolution of the cameras permitted all organisms larger than 50 mm to be reliably distinguished. In addition to the transects, previous ROV suction sampling at the nearby Akpo site (03°06.950' N 006°49.120' E) and a separate survey to carry out detailed video inspection of selected individual organisms aided species identifications (Jones *et al.*, 2006).

2.4. Data Analysis

Video transects were replayed at half speed and all visible organisms were counted along the entire transect. Fauna were identified to the highest taxonomic resolution possible, in some cases to species. Megafauna that could not be identified to species were grouped into morphologically distinguishable entities (referred to as taxa). It should be emphasised that this approach may underestimate the number of species present. Colonial organisms were counted as single individuals. Infaunal species were counted if enough of their body was visible for identification. Benthic fish were recorded but not included in subsequent quantitative analysis. Megafauna were classified into deposit and suspension feeders based on the literature descriptions.

Four indices of diversity were calculated in order to assess both the dominance and species richness aspects of diversity (Magurran 2003, Gotelli & Colwell 2001). These were the number of taxa in a transect or group of transects (a simple measure of species richness, S), rarefied species richness (estimated species in 60 individuals: $ES_{(60)}$), evenness (as measured by Pielou's evenness, J') and Shannon-Wiener species diversity (H' base log e). Numbers of organisms were expressed as abundances (numbers in each sampling unit) or as densities (no. m^{-2}). Diversity indices were calculated using PRIMER v6 (Clarke and Warwick, 2001).

The structure of the megabenthic assemblage was visualised using multidimensional scaling plots and sites compared using multivariate community analysis, specifically PERMANOVA (Anderson, 2001) and Multivariate dispersion analysis (Anderson, 2006). Multivariate community analysis was based on abundances of all taxa, a fourth root transformation being applied to buffer the influence of dominant taxa (Field *et al.*, 1982). Similarities were calculated using Bray-Curtis coefficients (Bray and Curtis, 1957). The similarity values were subjected to both classification (hierarchical group-average clustering) and ordination (non-metric multi-dimensional scaling) using the software PRIMER v6 (Clarke and Warwick, 2001). PERMANOVA and Multivariate dispersion analysis were carried out using the 'adonis' and 'betadisper' functions respectively using the R package Vegan (Oksanen *et al.*, 2011) in the R programming environment (R Development Core Team, 2010).

Data were analysed following one-way analysis of variance (ANOVA) design with slope as a fixed factor. This was implemented in the univariate case by generalised linear models and in the multivariate case by one-way PERMANOVA (Anderson, 2001). Independent generalised linear models were developed (Dobson and Barnett, 2008) to examine whether the taxon richness (number of species in a transect) and density (as numbers of epibenthic invertebrates in a transect) of both suspension and deposit feeding taxa could be explained by the seabed slope (treated as categorical data). The residual deviance for the count data (48.44 for suspension feeders; 97.26 for deposit feeders) was greater than the residual degrees of freedom (8 for both),

indicating overdispersion. The models were, therefore, fitted with quasi-Poisson errors. The models for species richness, evenness and species diversity were fitted with Gaussian errors. Models were fitted using the R function glm and the ANOVA function of the R package CAR (companion to applied regression) (Fox and Weisberg, 2011).

3. Results

The seabed was almost entirely composed of fine grain-sized sediment, no individual grains were visible in video (Figure 2), even when fully zoomed in. This suggested that the largest possible grain size is fine sand (< 0.5 mm) but observations of resuspension indicate that it was finer and classified as mud (< 125 μm). Hard substrata, composed of igneous rock (identified from samples), were visible within the areas of highest slope. These hard surfaces provided habitat for numerous specialist taxa (Table 1).

3.1. Nature of the benthic community

A total of 24 invertebrate megafaunal taxa representing six phyla were observed in the video transects at Usan (Table 1, Figure 3). In terms of species richness and numerical abundance, echinoderms were most abundant: 64% of the fauna were accounted for by 10 echinoderm taxa. Although eight cnidarian taxa were identified, they only represented 4% of the total density. Crustaceans were numerically important (31% total fauna) but only represented by three taxa, one of which, a galatheid, accounted for the vast majority of individuals. Of lesser importance were the poriferans, molluscs and enteropneusts, all with only one observed taxon and together representing <1% of the total invertebrates.

The regular echinothurid echinoid *Phormosoma placenta* was overwhelmingly dominant, particularly in the flatter areas, accounting for 53% of the invertebrates observed. Two other taxa were numerically important; the galatheid *Munidopsis* sp.

represented 29% of megafauna and an unidentified large ophiuroid represented 8%. The other taxa observed were each of low abundance (<3% of megafauna).

Although not considered further in this analysis, fish were observed at all the sites (S2). A small, dark-coloured, midwater gonostomatid fish was most abundant representing over 47 % of the fish fauna. The true benthic lophiiform *Dibranchus* sp. was common and represented 27% of the fish. The other major taxon was the nettastomatid anguilliform *Nettastoma melanura* which accounted for 18% of the fish. The demersal grenadier *Corphaenoides* sp. and the morid gadiform *Laenomena laureysi*? each represented around 2% of the fish seen in the video records.

3.2. Variation between habitats

3.2.1. Faunal density

Faunal density varied between habitats of different slope, with lower total densities in areas of higher slope. When total density is split into more ecologically meaningful units, based on feeding mode, the trends were even clearer (Figure 4). Deposit feeders made up the majority of the megafauna observed; however, when analysed alone, densities of deposit feeders decreased significantly with greater slopes (L-ratio = 16.09, d.f. = 3, $p < 0.01$). Densities of suspension feeders were very low except at the habitat with the highest slope; even here the density was less than half (0.17 m^{-2}) that of deposit feeders (0.40 m^{-2}). The increase in deposit feeder densities with slope was significant (L-ratio = 35.41, d.f. = 3, $p < 0.001$).

Of the major taxa, *Phormosoma placenta* had higher densities at low slope sites (L-ratio = 16.11, d.f. = 3, $p < 0.01$) as did the galatheid *Munidopsis* sp. (L-ratio = 88.37, d.f. = 3, $p < 0.001$). Ophiuroid densities were significantly higher in areas of higher slope (L-ratio = 24.88, d.f. = 3, $p < 0.001$).

294 3.2.2. Megafaunal diversity and assemblage structure

295

296 The slope-related differences in the habitat had a significant effect on the number of
297 taxa found (Figure 4; L-ratio = 9.33, d.f. = 3, $p < 0.05$). Pairwise tests, however, only
298 revealed significant differences between the habitat with the lowest slope (1°) and the
299 highest slope (29°). The principal difference in the diversity of sites was caused by the
300 presence of obligate epilithic species at the sites where hard substratum was exposed
301 (see Table 1). In soft sediment areas there was some variation in species complement
302 resulting from the apparently random presence or absence of rare species.

303

304 Species diversity indices (Figure 4) revealed that the species richness element of
305 diversity ($ES_{(60)}$: L-ratio = 35.42, d.f. = 3, $p < 0.001$) and the evenness component (J'
306 L-ratio = 66.14, d.f. = 3, $p < 0.001$) showed a highly significant positive linear
307 relationship with increasing slope of the habitat. As would be expected, a combined
308 index showed similar patterns with slope (H'; Figure 4). There were significant
309 pairwise differences between all the habitats ($p < 0.05$) in $ES_{(60)}$, J' and H' except
310 between 1 and 3 degrees in the combined Shannon-Wiener Index (p = ns).

311

312 Overall, multivariate community similarity was significantly different between
313 habitats of different slope (PERMANOVA: F = 9.55, d.f. = 1, 11, $p < 0.001$; Figure
314 5). Multivariate community similarity was high (> 60 %) and between-site dispersion
315 low between the habitats with lower slope (1, 3 and 11°), whereas the habitat with
316 highest slope (29°) was more heterogeneous (Multivariate dispersion analysis:
317 average distance to centroid 0.08 for 1°; 0.14 for 3°; 0.16 for 11° and 0.30 for 29°;
318 differences not significant in permutation test F = 2.57, d.f. = 3, p = 0.13). Two sites
319 (29B and 29C) formed a distinct group (with 77.5 % similarity) and one site (29A)
320 was intermediate between the highest and lower slope sites, having slightly higher
321 affinity with the lower slope sites (similarity 58.8%) than with the higher slope sites
322 (similarity 35.9%).

323

324 4. Discussion

325

326 4.1. General characteristics of the megafaunal assemblages at Usan

327

328 Knowledge of West African megafauna is limited, making it difficult to compare the
329 assemblage of invertebrates found at Usan to those at other locations. However, the
330 common species are known and the limited evidence suggests they are abundant off
331 West Africa. *Phormosoma placenta* is a common, often dominant, species on both
332 sides of the Atlantic (Jones and Brewer, 2012; Laguarda-Figueras *et al.*, 2005;
333 Sanchez *et al.*, 2008). The large ophuiroid observed at Usan is very similar to a
334 species found off Mauritania (Jones and Brewer, 2012), Ivory Coast and Angola
335 (author's observation; http://archive.serpentproject.com/151/), while a galatheid
336 resembling the species observed in the present study has been seen in images obtained
337 off Ivory Coast (Lebrato and Jones, 2009). It should be noted that even generic
338 differences are not always evident in photographs. The rarer species quantified in our
339 survey, and those seen outside the transect areas, likely include new species.
340 However, standard-resolution video and image data in general is not usually sufficient
341 to resolve the details necessary for species-level taxonomy.

342

343 The density of the megafaunal assemblages at Usan seems to be low, but in the range
344 of those found elsewhere (Figure 6). The nearest comparative area of an equivalent
345 depth is located off Ivory Coast where megafaunal densities were over three times
346 greater than at our study site. However, the Ivory Coast site experienced significantly
347 enhanced nutrient inputs from pyrosome carcasses (Lebrato and Jones, 2009). Few
348 other data are available for the East Atlantic at equivalent depths. Studies conducted
349 in deeper areas reported a range of megafaunal densities (Figure 6) that are usually
350 lower than at the Usan site. Of the deeper studies, only those areas that underlie
351 highly productive surface waters, for example the eutrophic EUMELI site off
352 Mauritania (Galeron *et al.*, 2000), have yielded comparable values.

353

354 4.2. Environmental consequences of differences in slope

355

Although four species were present at habitats with all the levels of slope investigated, ten of the taxa found at the habitat with the highest slope (29) were confined to this habitat. This habitat had exposed hard substrata and hence a unique community of epilithic megafauna. Most of the epilithic organisms were not found on soft sediments and many, for example gorgonians, had obvious morphological adaptations for attachment to rocky surfaces. Hard substratum communities are probably rare on the West African margin, having only been described off Mauritania where they are associated with corals (Colman *et al.*, 2005). Other studies of hard substrata near west Africa are on the mid-Atlantic ridge at non-vent (Gebruk *et al.*, 2010) and vent sites (Van Dover *et al.*, 2002), volcanic island groups, for example the Azores, or seamounts (Hall-Spencer *et al.*, 2007). The megafaunal assemblage found on hard substrata at Usan superficially resembles that found at non-vent hard substrata in the northern tropical Atlantic (in terms of faunal groups present) and from hard substrata in the deep sea in general (e.g. Lundsten *et al.*, 2009). However, without accurate species-level identifications either here or in the megafaunal literature generally, further patterns are difficult to assess.

The large reductions in density of deposit-feeding species at Usan with increases in habitat slope likely reflect reductions in food availability for deposit feeders. These patterns are unlikely to be related to the presence of hard substratum at the steepest slope site. Slope is expected to affect food availability in two ways. Firstly, increased slope will probably increase the lateral advection of food particles, reducing their residence times and hence availability for deposit feeders. Decreases in food availability have been repeatedly shown to be responsible for reductions in benthic megafaunal density in the deep sea (Galeron *et al.*, 2000; Thurston *et al.*, 1994). Secondly, increases in slope are likely to enhance local current speeds and hence lead to reductions in the deposition and increases in the winnowing of fine, nutritious particles (Levin *et al.*, 2001). Increased flow favours suspension feeding organisms over deposit feeders (Jumars and Nowell, 1984) and actively enhances recruitment, driving increased species density and elevated species richness (Palardy and Witman, 2011).

Increases in slope were associated with increased overall megafaunal diversity at Usan despite a decrease in the number of deposit-feeding species in the habitat with the steepest slopes. There was slightly (although not significantly) higher diversity, and consistent changes in multivariate community composition, in areas of steep slope without hard substrata. In the absence of other factors, reduced food availability tends to lead to reductions in diversity (Levin *et al.*, 2001; Waide *et al.*, 1999), as demonstrated in the tropical Atlantic deep sea (Cosson *et al.*, 1997). Organic particles are more likely to settle and become available for deposit feeders at low slopes (Fontanier *et al.*, 2008). At high slopes resuspension and current-mediated lateral transport of organic material is likely (Schlacher *et al.*, 2007; Van Gaever *et al.*, 2009), which may favour a suspension-feeding lifestyle. The trends in diversity observed at Usan are consistent with predictions based on food availability. Higher levels of organic matter may result in reduced diversity in areas, such as oxygen minimum zones, where the organic inputs are already high and associated with oxygen depletion (Levin *et al.*, 2001), which was not observed at Usan. In addition to influencing the organic content of the sediment, increases in slope are also likely to affect the substratum heterogeneity. Sediment grain size will likely become coarser and potentially more heterogeneous, increasing niche availability and hence deposit feeder diversity (Etter and Grassle, 1992; Wheatcroft, 1992), although this was not clear in the present study. In the Usan area the sites with steep slope have exposed hard substrata, presumably reflecting limited deposition. This increase in habitat heterogeneity is responsible for the clear and significant increases in diversity and changes in multivariate community composition at the steepest slope sites. An entirely different range of animals is able to colonise hard substrata and hence, where this is present, diversity is likely to increase (Levin *et al.*, 2001).

Deep-sea biology requires more detailed local-scale studies of faunal distribution in relation to habitat features. Physical gradients in biological assemblages associated with slope occur in many ecosystems (de Castilho *et al.*, 2006); this study extends these findings to the African deep sea. Considerable areas of the ocean margins have features of high topography and sloping seabed, such as described here. This study has shown clear reductions in deposit-feeding megafaunal density with slope. If this trend is typical for deep-water habitats, it should be incorporated into model estimates

421 of megafaunal densities, particularly on areas of elevated topography. Diversity of
422 benthic megafauna does not display such a clear relationship with slope and is likely
423 to be controlled by site-specific responses to changes in habitat heterogeneity and
424 food availability.

425

426 5. Acknowledgements

427

428 The authors thank Total E&P Nigeria and the Total Foundation for supporting this
429 work. We thank Stephen Cairns (cnidarians), Kenneth Sulak (fish) and Sven Thatje
430 (crustaceans) for help with species identification. We acknowledge Alex Ugwumba
431 and Adesina Adegbie for participating in the project. Thanks are due to the University
432 of Ibadan, Nigeria, and the Institute for Oceanography and Marine Research, Lagos,
433 Nigeria for providing personnel for the survey. This study would have been
434 impossible without the help of the captain and crew of the *Bourbon Diamond*
435 including the Oceaneering ROV team (Stuart Jones, David Cox, Jayselan Naidoo,
436 Usif Abdulatif, Neil Purdie, Steve Fisher and Michael Clark). This work was carried
437 out as part of the SERPENT Project www.serpentproject.com. This work was funded
438 in part by the UK Natural Environment Research Council as part of the Marine
439 Environmental Mapping Programme (MAREMAP).

440

441 6. References
442
443 Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of
444 variance. Austral Ecology 26 (1), 32-46.

445 Anderson, M.J., 2006. Distance-based tests for homogeneity of multivariate
446 dispersions. Biometrics 62 (1), 245–253.

447 Baguley, J.G., Montagna, P.A., Hyde, L.J., Kalke, R.D., Rowe, G.T., 2006. Metazoan
448 meiofauna abundance in relation to environmental variables in the northern Gulf of
449 Mexico deep sea. Deep-Sea Research Part I-Oceanographic Research Papers 53 (8),
450 1344-1362.

451 Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest of southern
452 Wisconsin. Ecological Monographs 27, 225-349.

453 Butman, C.A., 1990. Sediment-trap experiments on the importance of
454 hydrodynamical processes in distributing settling invertebrate larvae in near-bottom
455 waters. Journal of Experimental Marine Biology and Ecology 134 (1), 37-88.

456 Butman, C.A., Frechette, M., Geyer, W.R., Starczak, V.R., 1994. Flume experiments
457 on food supply to the blue mussel *Mytilus edulis* L. as a function of boundary-layer
458 flow. Limnology and Oceanography 39 (7), 1755-1768.

459 Clark, M.R., Rowden, A.A., Schlacher, T., Williams, A., Consalvey, M., Stocks, K.I.,
460 Rogers, A.D., O'Hara, T.D., White, M., Shank, T.M., Hall-Spencer, J.M., 2010. The
461 Ecology of Seamounts: Structure, Function, and Human Impacts. Annual Review of
462 Marine Science, pp. 253-278.

463 Clarke, K.R., Warwick, R.M., 2001. Changes in marine communities: an approach to
464 statistical analysis and interpretation. Plymouth Marine Laboratory, U.K.

465 Colman, J.G., Gordon, D.M., Lane, A.P., Forde, M.J., Fitzpatrick, J.J., 2005.
466 Carbonate mounds off Mauritania, north-west Africa: status of deep-water corals and
467 implications for management of fishing and oil exploration activities. In: Freiwald,
468 A., Roberts, J.M. (Eds.), Cold-Water Corals and Ecosystems. Springer-Verlag, Berlin,
469 pp. 417-441.

Cosson, N., Sibuet, M., Galeron, J., 1997. Community structure and spatial heterogeneity of the deep-sea macrofauna at three contrasting stations in the tropical northeast Atlantic. Deep-Sea Research 44, 247-269.

de Castilho, C.V., Magnusson, W.E., de Araújo, R.N.O., Luizão, R.C.C., Luizão, F.J., Lima, A.P., Higuchi, N., 2006. Variation in above-ground tree live biomass in a central Amazonian forest: effects of soil and topography. Forest Ecology and Management 234 (1-3), 85-96.

De Leo, F.C., Smith, C.R., Rowden, A.A., Bowden, D.A., Clark, M.R., 2010. Submarine canyons: hotspots of benthic biomass and productivity in the deep sea. Proceedings of the Royal Society B-Biological Sciences 277 (1695), 2783-2792.

Dobson, A.J., Barnett, A.G., 2008. An Introduction to Generalized Linear Models. Chapman & Hall, London.

Duineveld, G.C.A., Lavaleye, M.S.S., Noort, G.J.v., 1993a. The trawlfauna of the Mauritanian shelf (Northwest Africa): Density, species composition, and biomass. Hydrobiologia 258 (1-3), 165-173.

Duineveld, G.C.A., Wilde, P., Berghuis, E.M., Kok, A., 1993b. The benthic infauna and benthic respiration off the Banc d'Arguin (Mauritania, Northwest Africa). Hydrobiologia 258 (1-3), 107-117.

Etter, R.J., Grassle, J.F., 1992. Patterns of species diversity in the deep sea as a function of sediment particle size diversity. Nature 360 (6404), 576-578.

FAO Fishery Committee for the Eastern Central Atlantic, 1991. The "Guinea 90" survey. Food and Agriculture Organization of the United Nations, Rome.

Field, J.G., Clarke, K.R., Warwick, R.M., 1982. A practical strategy for analysing multispecies distribution patterns. Marine Ecology Progress Series 8, 37-52.

Fontanier, C., Jorissen, F.J., Lansard, B., Mouret, A., Buscail, R., Schmidt, S., Kerherve, P., Buron, F., Zaragosi, S., Hunault, G., Ernoult, E., Artero, C., Anschutz, P., Rabouille, C., 2008. Live foraminifera from the open slope between Grand Rhone

497 and Petit Rhone Canyons (Gulf of Lions, NW Mediterranean). Deep-Sea Research
498 Part I-Oceanographic Research Papers 55 (11), 1532-1553.

499 Fox, J., Weisberg, S., 2011. An {R} Companion to Applied Regression, Second
500 Edition. . Sage, Thousand Oaks CA.

501 Gage, J.D., 1997. High benthic species diversity in deep-sea sediments: The
502 importance of hydrodynamics. In: Ormond, R.F.G., Gage, J.D., Angel, M.V. (Eds.),
503 Marine Biodiversity. Cambridge University Press, Cambridge, UK, pp. 148-177.

504 Galeron, J., Sibuet, M., Mahaut, M.L., Dinet, A., 2000. Variation in structure and
505 biomass of the benthic communities at three contrasting sites in the tropical Northeast
506 Atlantic. Marine Ecology-Progress Series 197, 121-137.

507 Gebruk, A., Budaeva, N.E., King, N., 2010. Bathyal benthic fauna of the Mid-Atlantic
508 Ridge between the Azores and the Reykjanes Ridge. Journal of the Marine Biological
509 Association of the United Kingdom 90 (1), 1-14.

510 Genin, A., Dayton, P.K., Lonsdale, P.F., Spiess, F.N., 1986. Corals on seamount
511 peaks provide evidence of current acceleration over deep-sea topography. Nature 322
512 (6074), 59-61.

513 Hall-Spencer, J., Rogers, A., Davies, J., Foggo, A., 2007. Deep-sea coral distribution
514 on seamounts, oceanic islands, and continental slopes in the Northeast Atlantic.
515 Conservation and Adaptive Management of Seamount and Deep-Sea Coral
516 Ecosystems, 135-146.

517 Helly, J., Levin, L., 2004. Global distribution of naturally occurring marine hypoxia
518 on continental margins. Deep Sea Research Part I: Oceanographic Research Papers 51
519 (9), 1159-1168.

520 Henriques, C., Priede, I.G., Bagley, P.M., 2002. Baited camera observations of deep-
521 sea demersal fishes of the northeast Atlantic Ocean at 15-28 degrees N off West
522 Africa. Marine Biology 141 (2), 307-314.

523 Jones, D.O.B., 2009. Using existing industrial remotely operated vehicles for deep-sea
524 science. Zoologica Scripta 38 (s1), 41-47.

525 Jones, D.O.B., Brewer, M.E., 2012. Response of megabenthic assemblages to
526 different scales of habitat heterogeneity on the Mauritanian slope. Deep Sea Research
527 Part I: Oceanographic Research Papers 67, 98-110.

528 Jones, D.O.B., Hudson, I.R., Bett, B.J., 2006. Effects of physical disturbance on the
529 cold-water megafaunal communities of the Faroe-Shetland Channel. Marine Ecology
530 Progress Series 319, 43-54.

531 Jumars, P.A., Nowell, A.R.M., 1984. Fluid and Sediment Dynamic Effects on Marine
532 Benthic Community Structure. American Zoologist 24 (1), 45-55.

533 Keller, N.B., Pasternak, F.A., 2002. Madreporic and Gorgonian corals (Anthozoa:
534 Scleractinia, Gorgonacea) in the benthos of the African shelf and slope in the Canary
535 upwelling area. Oceanology 42(4), 521-525.

536 Kroncke, I., Turkay, M., 2003. Structural and functional aspects of the benthic
537 communities in the deep Angola Basin. Marine Ecology Progress Series 260, 43-53.

538 Laguarda-Figueras, A., Gutierrez-Castro, A.I., Solis-Marin, F.A., Duran-Gonzalez,
539 A., Torres-Vega, J., 2005. Echinoids (Echinodermata : Echinoidea) from the Gulf of
540 Mexico. Revista De Biologia Tropical 53, 69-108.

541 Le Loeuff, P., 1993. The benthic fauna of the Guinea continental shelf (trawling
542 grounds), compared to the fauna of the Cote-D'Ivoire. Revue d'Hydrobiologie
543 Tropicale 26 (3), 229-252.

544 Le Loeuff, P., von Cosel, R., 1998. Biodiversity patterns of the marine benthic fauna
545 on the Atlantic coast of tropical Africa in relation to hydroclimatic conditions and
546 paleogeographic events. Acta Oecologica-International Journal of Ecology 19 (3),
547 309-321.

548 Lebrato, M., Jones, D.O.B., 2009. Mass deposition event of *Pyrosoma atlanticum*
549 carcasses off Ivory Coast (West Africa). Limnology and Oceanography 54 (4), 1197-
550 1209.

551 Leichter, J.J., Witman, J.D., 1997. Water flow over subtidal rock walls: Relation to
552 distributions and growth rates of sessile suspension feeders in the Gulf of Maine -

553 Water flow and growth rates. Journal of Experimental Marine Biology and Ecology
554 209 (1-2), 293-307.

555 Levin, L.A., Dayton, P.K., 2009. Ecological theory and continental margins: where
556 shallow meets deep. Trends in Ecology & Evolution 24 (11), 606-617.

557 Levin, L.A., Etter, R.J., Rex, M.A., Gooday, A.J., Smith, C.R., Pineda, J., Stuart,
558 C.T., Hessler, R.R., Pawson, D., 2001. Environmental influences on regional deep-sea
559 species diversity. Annual Review of Ecology and Systematics 32, 51-93.

560 Levin, L.A., Gooday, A.J., 2001. The deep Atlantic Ocean. In: Tyler, P.A. (Ed.),
561 Ecosystems of the world: Vol. 28. Ecosystems of Deep Oceans. Elsevier, Amsterdam.

562 Lundblad, E.R., Wright, D.J., Miller, J., Larkin, E.M., Rinehart, R., Naar, D.F.,
563 Donahue, B.T., Anderson, S.M., Battista, T., 2006. A Benthic Terrain Classification
564 Scheme for American Samoa. Marine Geodesy 29 (2), 89 - 111.

565 Lundsten, L., Barry, J.P., Cailliet, G.M., Clague, D.A., DeVogelaere, A.P., Geller,
566 J.B., 2009. Benthic invertebrate communities on three seamounts off southern and
567 central California, USA. Marine Ecology Progress Series 374, 23-32.

568 MacArthur, R.H., Wilson, E.O., 1967. The theory of island biogeography. Princeton
569 University Press, Princeton.

570 Merrett, N.R., Domanski, P.A., 1985. Observations on the ecology of deep-sea
571 bottom-living fishes collected off northwest Africa: II. The Moroccan Slope (27-
572 34N), with special reference to *Synaphobranchus kaupi*. Biological Oceanography 3
573 (4), 349-399.

574 Merrett, N.R., Marshall, N.B., 1981. Observations on the ecology of deep-sea bottom-
575 living fishes collected off northwest Africa (08-27N). Progress in Oceanography 9
576 (4), 185-244.

577 Noble, M., Mullineaux, L.S., 1989. Internal tidal currents over the summit of Cross
578 Seamount. Deep Sea Research 36, 1791-1802.

579 Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., O'Hara, R.B., Simpson, G.L.,
580 Solymos, P., Stevens, M.H.H., Wagner, H., 2011. vegan: Community Ecology
581 Package. R package version 1.17-9. http://CRAN.R-project.org/package=vegan.

582 Palardy, J.E., Witman, J.D., 2011. Water flow drives biodiversity by mediating rarity
583 in marine benthic communities. Ecology Letters 14 (1), 63-68.

584 R Development Core Team, 2010. R: A language and environment for statistical
585 computing. R Foundation for Statistical Computing. ISBN 3-900051-07-0, URL
586 http://www.R-project.org., Vienna, Austria.

587 Roeleveld, M.A.C., Lipinski, M.R., Augustyn, C.J., Stewart, B.A., 1992. The
588 distribution and abundance of cephalopods on the continental-slope of the Eastern
589 South-Atlantic. South African Journal of Marine Science-Suid-Afrikaanse Tydskrif
590 Vir Seewetenskap 12, 739-752.

591 Rowe, G.T., Polloni, P.T., Haedrich, R.L., 1982. The deep-sea macrobenthos of the
592 continental margin of the Northwest Atlantic Ocean. Deep-Sea Research Part a-
593 Oceanographic Research Papers 29 (2), 257-278.

594 Roy, K.O.L., Caprais, J.C., Fifis, A., Fabri, M.C., Galeron, J., Budzinsky, H., Le
595 Menach, K., Khripounoff, A., Ondreas, H., Sibuet, M., 2007. Cold-seep assemblages
596 on a giant pockmark off West Africa: spatial patterns and environmental control.
597 Marine Ecology-an Evolutionary Perspective 28 (1), 115-130.

598 Saiz-Salinas, J.I., 2007. Sipunculans and echiurans from the deep Angola Basin.
599 Journal of Natural History 41 (45-48), 2789-2800.

600 Sanchez, F., Serrano, A., Parra, S., Ballesteros, M., Cartes, J.E., 2008. Habitat
601 characteristics as determinant of the structure and spatial distribution of epibenthic
602 and demersal communities of Le Danois Bank (Cantabrian Sea, N. Spain). Journal of
603 Marine Systems 72 (1-4), 64-86.

604 Schaff, T., Levin, L.A., Blair, N.E., DeMaster, D.J., Pope, R., Boehme, S.E., 1992.
605 Spatial heterogeneity of benthos on the Carolina continental slope: large (100 km)-
606 scale variation. Marine Ecology Progress Series 88, 143−160.

607 Scheren, P.A., Ibe, A.C., Janssen, F.J., Lemmens, A.M., 2002. Environmental
608 pollution in the Gulf of Guinea - a regional approach. Marine Pollution Bulletin 44
609 (7), 633-641.

610 Schlacher, T.A., Schlacher-Hoenlinger, M.A., Williams, A., Althaus, F., Hooper,
611 J.N.A., Kloser, R., 2007. Richness and distribution of sponge megabenthos in
612 continental margin canyons off southeastern Australia. Marine Ecology-Progress
613 Series 340, 73-88.

614 Sebens, K.P., 1985. Community ecology of vertical rock walls in the Gulf of Maine,
615 USA.: Small-scale processes and alternative community states. In: Moore, P.G., Seed,
616 R. (Eds.), The Ecology of Rocky Coasts. Hodder and Stoughton.

617 Simpson, E.H., 1949. Measurement of diversity. Nature 163, 688.

618 Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M.,
619 Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity:
620 the importance of keystone structures. Journal of Biogeography 31 (1), 79-92.

621 Thandar, A.S., 1999. Deep-sea holothuroids taken by the R.V. Africana II in 1959,
622 from off the west coast of the Cape Peninsula, South Africa. Annals of the South
623 African Museum 105 (9), 363-409.

624 Thurston, M.H., Bett, B.J., Rice, A.L., Jackson, P.A.B., 1994. Variations in the
625 invertebrate abyssal megafauna in the North Atlantic Ocean. Deep-Sea Research Part
626 I: Oceanographic Research Papers 41 (9), 1321-1348.

627 Total E. & P. Nigeria Ltd., 2007. Usan (OPL 222) development environmental
628 baseline study: Usan field and pipeline route. Biogeochem associates limited, Port
629 Harcourt, Nigeria.

630 Tyler, P.A., 1995. Conditions for the existence of life at the deep sea floor: An update.
631 Oceanography and Marine Biology: An Annual Review 33, 221-244.

632 Uriz, M.-J., 1988. Deep-water sponges from the continental shelf and slope off
633 Namibia (southwest Africa): classes Hexactinellida and Demospongia. Monografias
634 de Zoologia Marina 3, 9-157.

635 Van Dover, C.L., German, C.R., Speer, K.C., Parson, L.M., Vrijenhoek, R.C., 2002.
636 Evolution and biogeography of deep-sea vent and seep invertebrates. Science 295,
637 1253-1257.

638 Van Gaever, S., Galéron, J., Sibuet, M., Vanreusel, A., 2009. Deep-sea habitat
639 heterogeneity influence on meiofaunal communities in the Gulf of Guinea. Deep Sea
640 Research Part II: Topical Studies in Oceanography 56 (23), 2259-2269.

641 Vinogradova, N.G., Galkin, S.W., Kamenskaja, O.E., Levenstein, R.Y., Romanov,
642 V.N., 1990. The distribution of the deep sea bottom fauna in the transoceanic section
643 in the south Atlantic Ocean along 31° 30'. Transactions of the P. P. Shirshov Institute
644 of Oceanology 126, 7-19.

645 Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., 1999. The
646 relationship between productivity and species richness. Annual Review of Ecology
647 and Systematics 30, 257-300.

648 Wheatcroft, R.A., 1992. Experimental tests for particle size-dependent bioturbation in
649 the deep ocean. Limnology and Oceanography 37 (1), 90-104.

650 Williams, A., Althaus, F., Dunstan, P.K., Poore, G.C.B., Bax, N.J., Kloser, R.J.,
651 McEnnulty, F.R., 2010. Scales of habitat heterogeneity and megabenthos biodiversity
652 on an extensive Australian continental margin (100–1100 m depths). Marine Ecology
653 31 (1), 222-236.

654 Wilson, M.F.J., O'Connell, B., Brown, C., Guinan, J.C., Grehan, A.J., 2007.
655 Multiscale Terrain Analysis of Multibeam Bathymetry Data for Habitat Mapping on
656 the Continental Slope. Marine Geodesy 30 (1), 3 - 35.

657 Zabanbark, A., 2002. Passive continental margins of West Africa and unusual features
658 of the oil and gas potential of their deep-water part. Oceanology 42 (2), 291-297.

659 Zibrowius, H., Gili, J.-M., 1990. Deep-water scleractinia (Cnidaria: Anthozoa) from
660 Namibia, South Africa, and Walvis Ridge, southeastern Atlantic. Scientia Marina 54
661 (1), 19-46.
662
663

Table 1: Invertebrate megafauna densities (no m^{-2}) at each transect at Usan. Slope is represented by numbers: 1 = 1°, 3 = 3°, 11 = 11°, 29 = 29°. Site letters represent replicates. Asterisked taxa (*) are known to prefer hard substrata and double asterisked (**) only live on hard substrata (obligately epilithic). Deposit feeders (D) and suspension feeders (S) are labelled. See figure 3 for images of the taxa.

	1A	1B	1C	3A	3B	3C	11A	11B	11C	29A	29B	29C
Hexactinellid**S	0	0	0	0	0	0	0	0	0	0	0.006	0.003
White antipatharian**S	0	0	0	0	0	0	0	0	0	0	0.047	0.061
Whip-like cnidarian (sand) S	0	0	0	0	0.003	0	0.003	0.003	0.003	0	0	0
Whip-like cnidarian (rock, white)** S	0	0	0	0	0	0	0	0	0	0	0.009	0.009
Pennatulea sp. S	0	0	0	0	0	0	0	0	0	0	0.006	0
Gorgonian fan** S	0	0	0	0	0	0	0	0	0	0	0	0.009
Actinoscypha sp.	0.003	0	0.003	0	0	0	0	0	0	0	0	0
Edwardsiid anemone	0	0	0.003	0	0	0	0	0	0	0	0	0
Striped anemone	0	0	0.003	0.003	0	0.003	0	0	0	0	0	0
Phormosoma placenta D	0.343	0.395	0.302	0.140	0.233	0.352	0.201	0.009	0.012	0.090	0.023	0.081
Red echinoid	0	0	0	0	0	0	0	0	0	0.003	0.012	0.003
White echinoid	0	0	0	0	0	0	0	0	0	0.003	0	0.003
White *Diadema* sp.	0	0	0	0	0	0	0	0	0	0.003	0.009	0.006
Ophiuroid D	0.012	0	0	0.009	0.020	0.032	0.064	0.070	0.038	0.029	0.052	0.026
Brisingid* S	0	0	0	0	0	0	0	0	0	0	0.012	0.003
Holothurian D	0.012	0.003	0	0	0.003	0.003	0	0	0	0	0	0
Mesothuria sp. D	0	0.009	0.006	0.003	0	0	0.003	0.003	0.017	0	0	0
Benthothuria sp. D	0	0	0	0.006	0	0	0	0	0.003	0.003	0	0
Commatulid* S	0	0	0	0	0	0	0	0	0	0	0.003	0
Galatheid	0.090	0.070	0.047	0.142	0.180	0.116	0.180	0.172	0.172	0.032	0.006	0.015
Prawn	0.003	0.009	0.015	0.003	0.009	0.003	0.006	0.003	0.009	0.012	0	0
c.f. *Nephrops* sp.?	0	0	0	0.003	0.003	0	0.003	0.003	0	0	0	0
Opisthobranch D	0	0	0	0.003	0	0	0	0	0	0	0	0
Enteropneust D	0	0	0	0	0	0	0	0	0.003	0	0	0
TOTAL	0.462	0.485	0.378	0.311	0.451	0.509	0.459	0.262	0.256	0.174	0.183	0.218
Total suspension feeders	0	0	0	0	0.003	0	0.003	0.003	0.003	0	0.081	0.084
Total deposit feeders	0.456	0.477	0.355	0.302	0.436	0.503	0.448	0.253	0.244	0.154	0.081	0.122

FIGURES

Figure 1: Bathymetry of Usan area showing the position of ROV seabed transects. The lower panel shows the higher slope transects in more detail. The inset on the upper panel shows the position of the study site in the Gulf of Guinea. The length of the 200 m long ROV transects is drawn to scale.

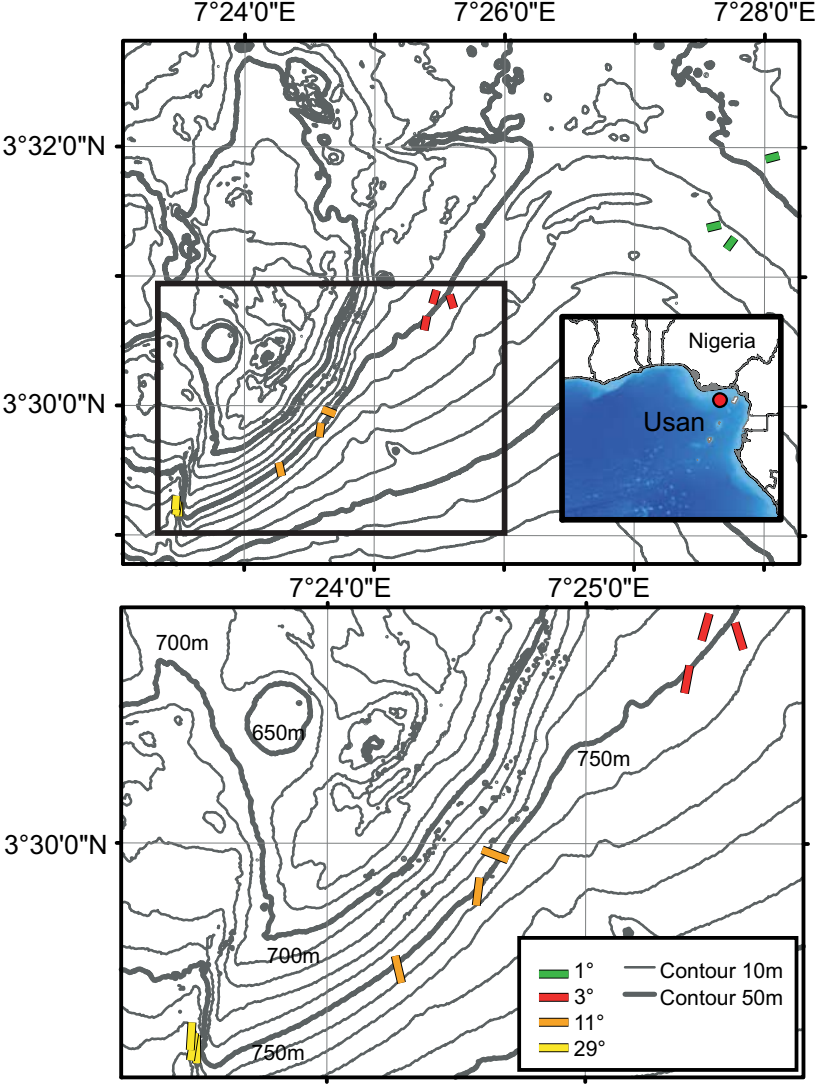
Figure 2: Example pictures of seabed habitats with different slope found at Usan: A) 1° slope, B) 3° slope, C) 11° slope, D) soft-substratum area with 29° slope and E) hard-substratum area with 29° slope. Images A to D are images from the video transects cropped to show an approximately 0.5 m wide section of seafloor at the base of the image. Image E is a more oblique image cropped to show an approximately 1 m wide section of seafloor at the base of the image.

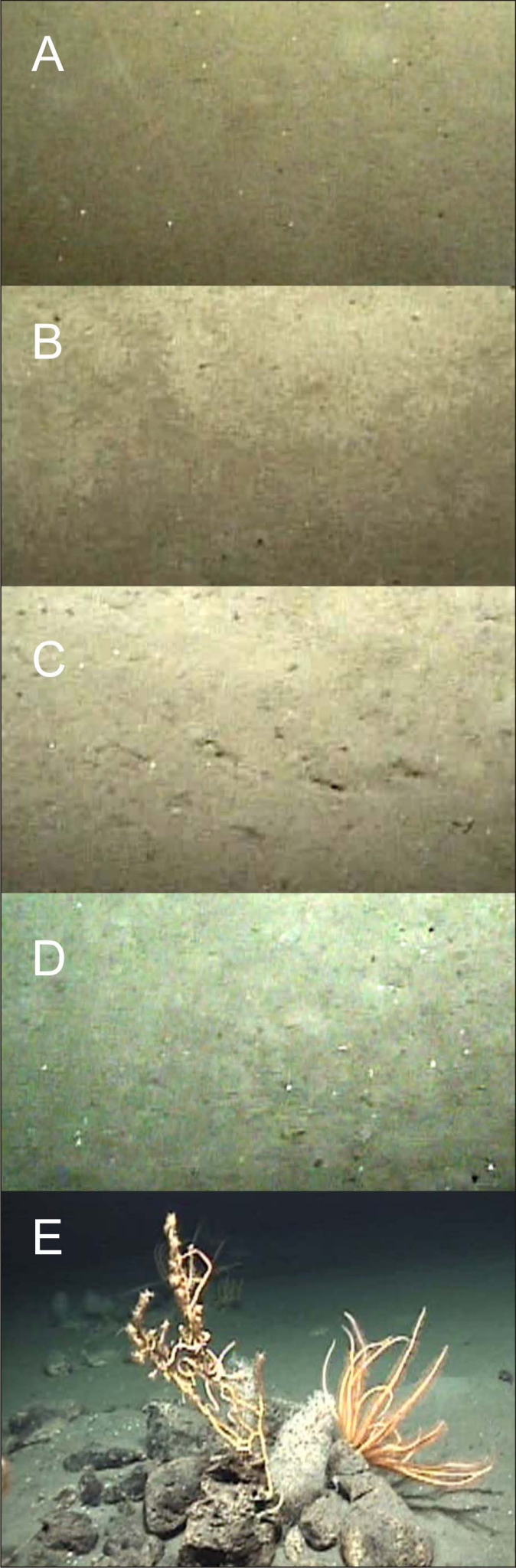
Figure 3: Examples of megafauna found at Usan: A) Hexactinellid (~150 mm diameter), B) White antipatharian (~200 mm height), C) Whip-like cnidarian (found on rocks, ~ 400 mm height), D) Whip-like cnidarian (found on sand, ~ 300 mm height), E) Gorgonian fan (~ 1m height), F) *Pennatulea* sp. (~300 mm height), G) Brisingid (arm length ~ 250mm), H) *Phormosoma placenta* (50-120 mm diameter), I) Red echinoid (70 mm diameter), J) White *Diadema* sp. (~150 mm diameter including spines), K) Ophiuroid (~150 mm arm-tip to arm-tip), L) Galatheid (up to 100 mm length), M) *Prawn (~100 mm total length), N) *Cerianthid? (~ 100 mm total diameter), O & P) *Lithodid crab (c.f. *Paralomis cristulata*, ~100 carapace width). * species observed but not seen in quantitative transects.

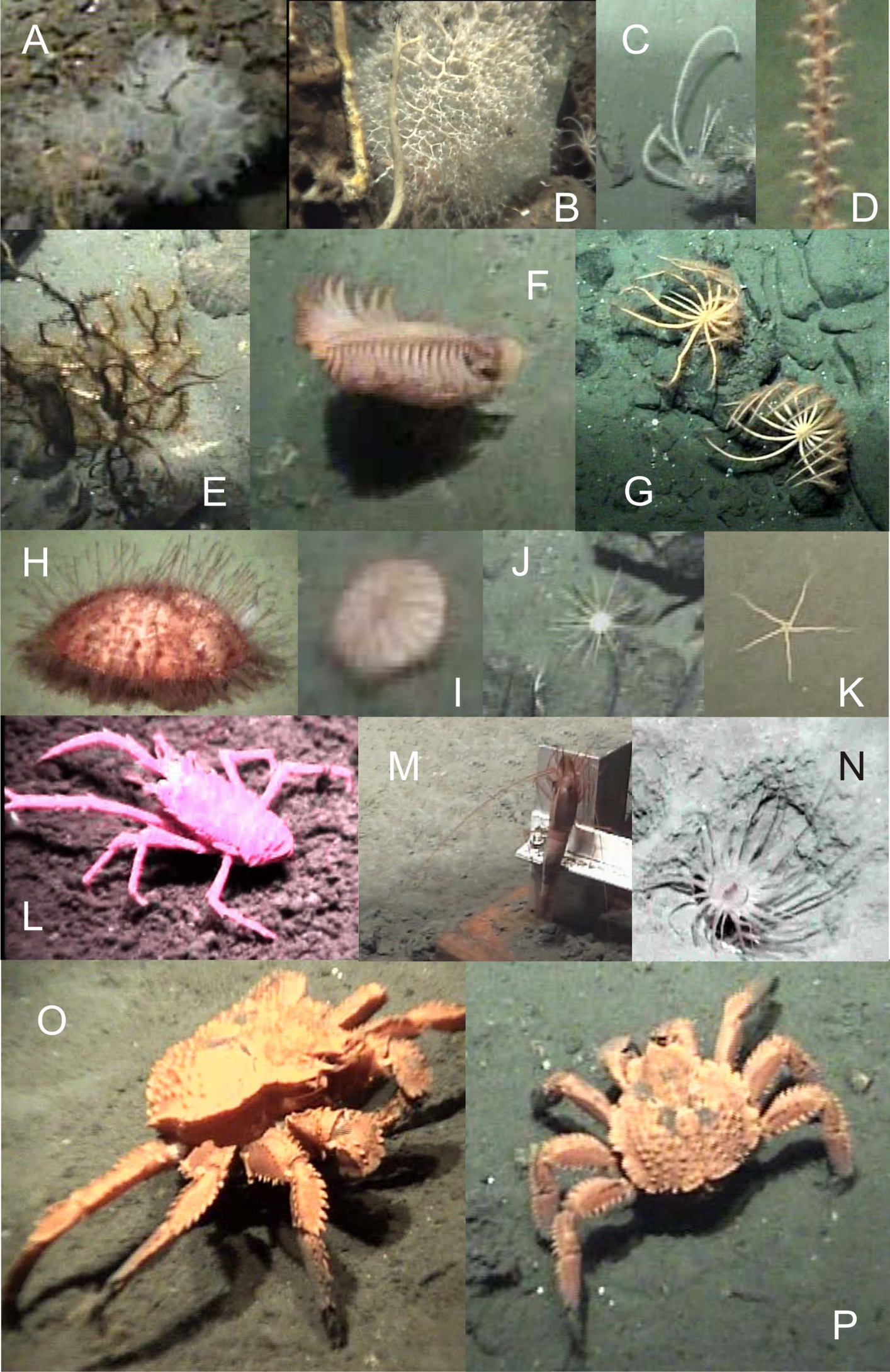
Figure 4: Response of megafaunal assemblage indices to slope at the Usan area, offshore Nigeria. A) Megafaunal invertebrate deposit (hollow circles) and suspension feeding (filled circles) assemblage total densities. B) Number of megafaunal invertebrate deposit (hollow circles) and suspension feeding (filled circles) taxa. C) Evenness of entire invertebrate megafaunal assemblage measured by Pielou's evenness (J'). D) Shannon-Wiener (log base e) combined diversity index (H') of entire invertebrate megafaunal assemblage. Errors bars on all graphs represent standard deviations and points represent the mean density of 3 replicates. For A) and B) the megafauna was separated into deposit (hollow circles) and suspension (filled circles) feeders.

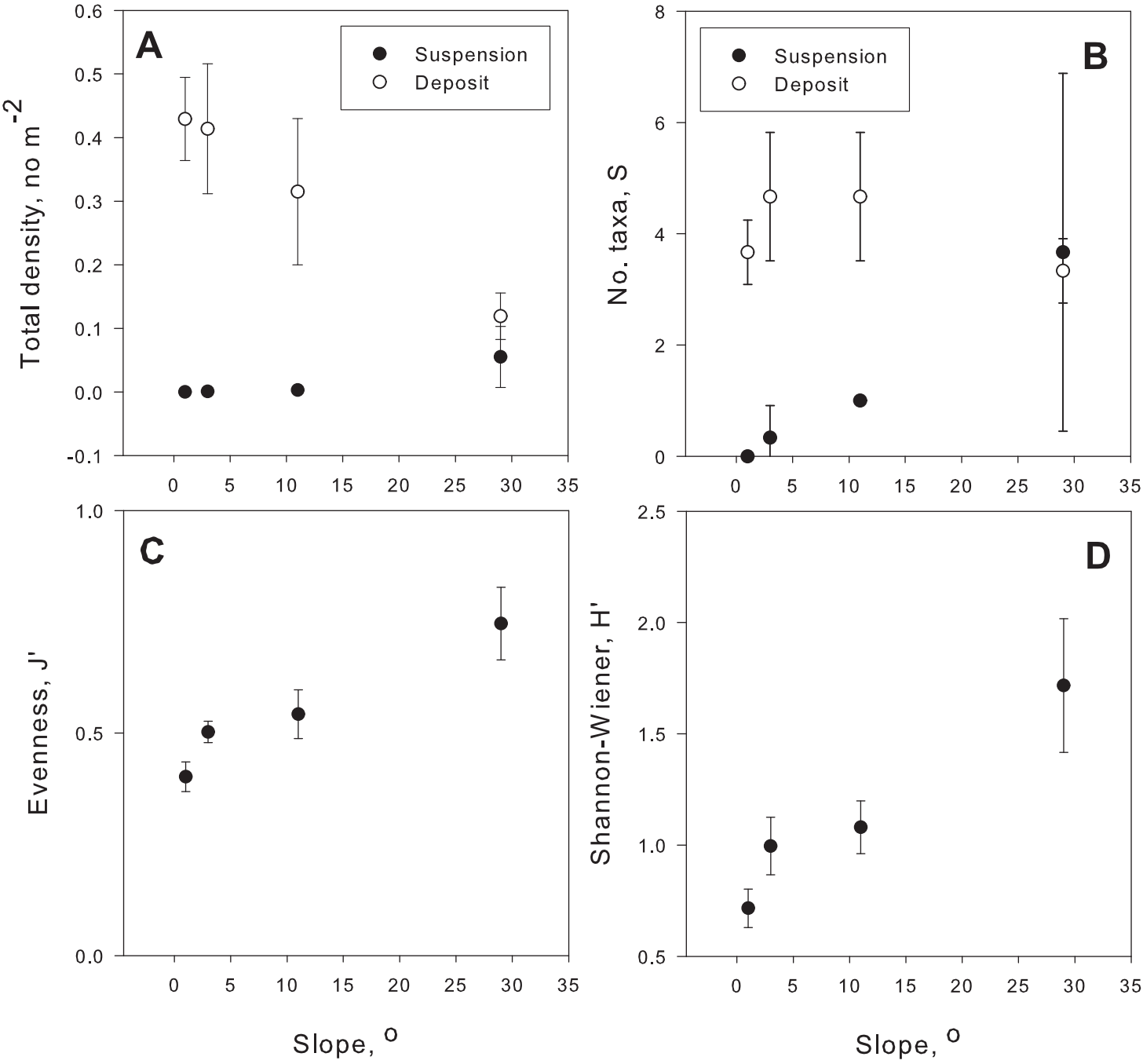
Figure 5: Multidimensional Scaling Ordination of Bray-Curtis similarities (4th root transformed) of Usan Invertebrate megafaunal assemblage. Overlaid are similarity levels from hierarchical cluster analysis (as percentages). Slope is represented by numbers equating to the slope in degrees. Letters represent replicates.

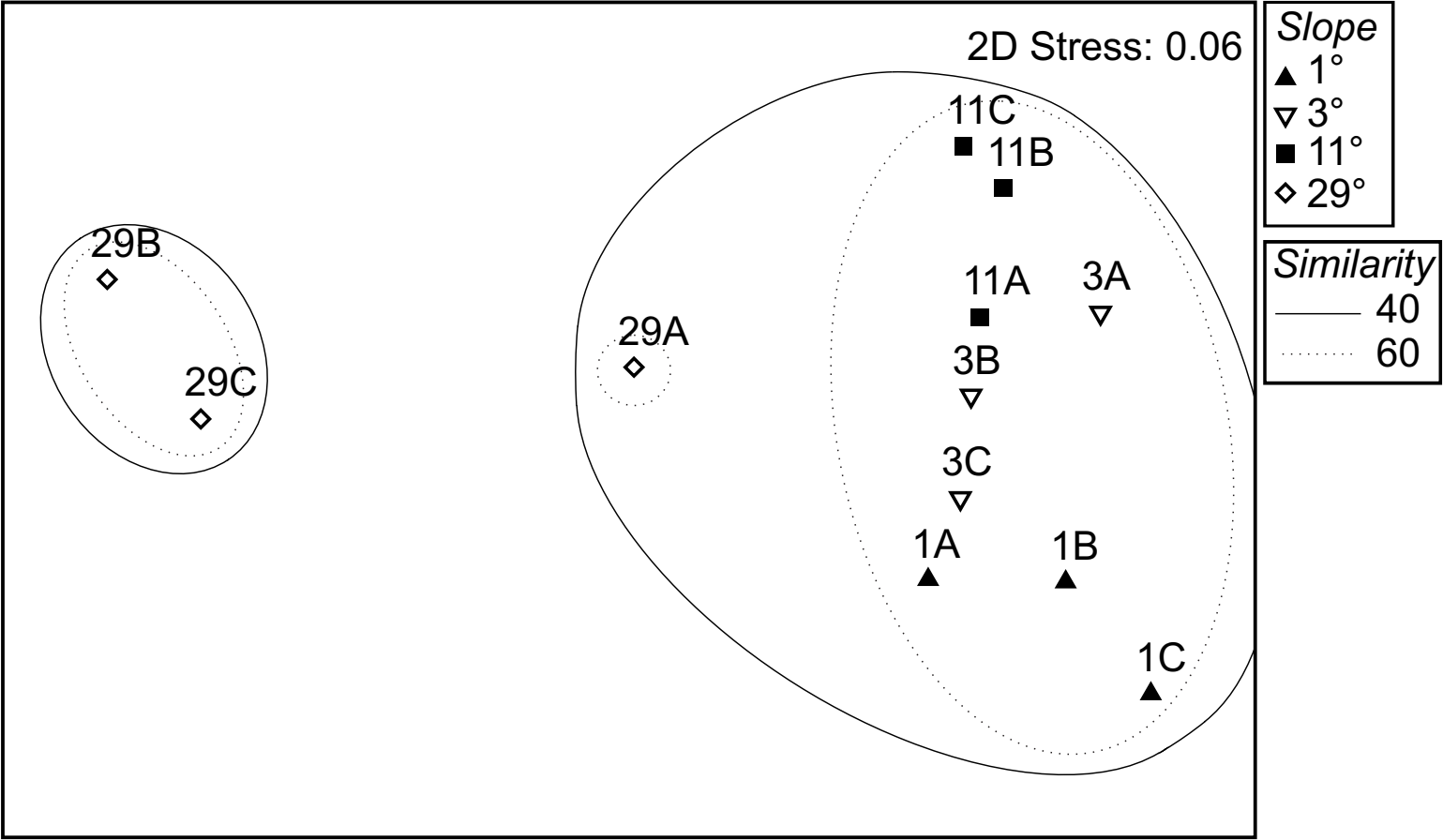
Figure 6: Megafaunal density (no hectare^{-1}) compared with depth for the Eastern Atlantic. East Atlantic literature data from Bay of Biscay south to Angola (Feldt *et al.*, 1989; Galeron *et al.*, 2000; Kroncke and Turkay, 2003; Lebrato and Jones, 2009; Sibuet *et al.*, 1989; Sibuet *et al.*, 1984; Sibuet and Segonzac, 1985; Thurston *et al.*, 1994; Tietjen, 1992)

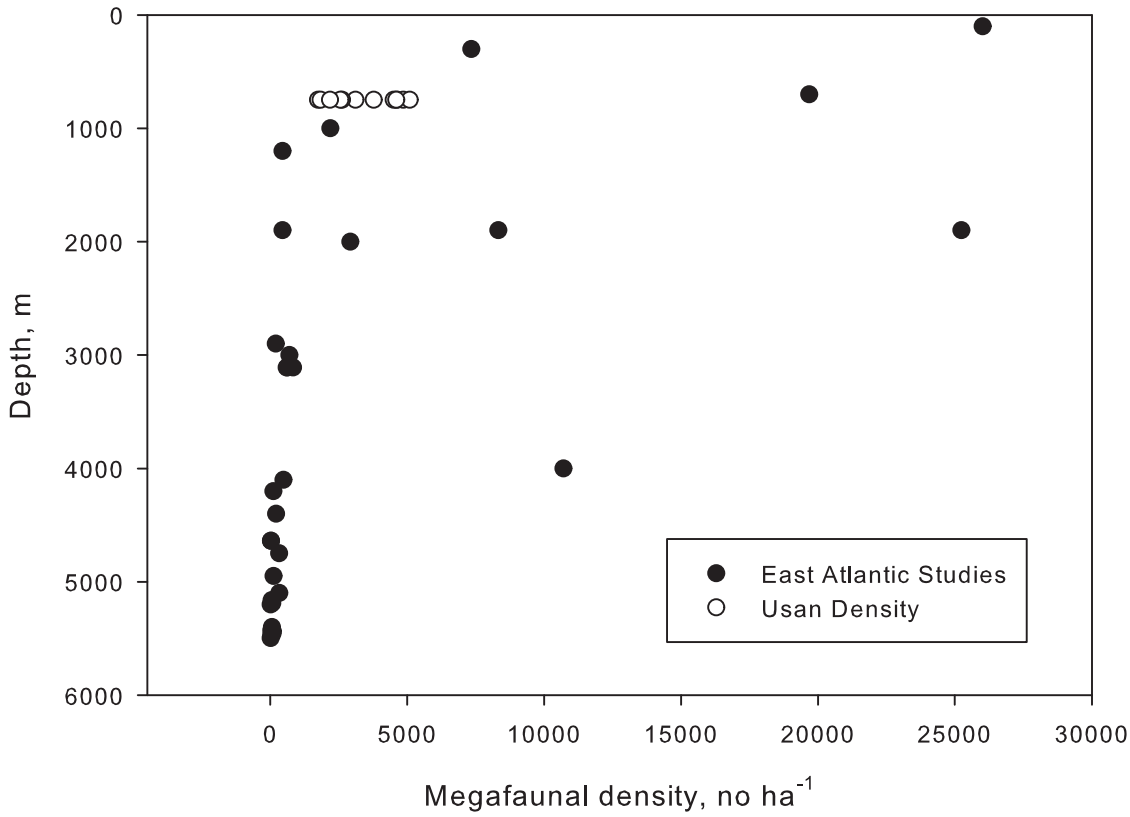

7°24'0"E
7°26'0"E
7°28'0"E
3°32'0"N
3°30'0"N
Nigeria
Usan
7°24'0"E
7°25'0"E
3°30'0"N
700m
650m
750m
700m
750m
1°
3°
11°
29°
Contour 10m
Contour 50m


A
B
C
D
E


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P


A
Suspension
Deposit
Total density, no m-2
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
0
5
10
15
20
25
30
35
B
Suspension
Deposit
No. taxa, S
8
6
4
2
0
C
Evenness, J'
1.0
0.5
0.0
Slope, o
D
Shannon-Wiener, H'
2.5
2.0
1.5
1.0
0.5
Slope, o


2D Stress: 0.06
Slope
1°
3°
11°
29°
Similarity
40
60
11C
11B
11A
3A
29A
3B
3C
1A
1B
1C
29B
29C


0
1000
2000
3000
4000
5000
6000
Depth, m
0
5000
10000
15000
20000
25000
30000
Megafaunal density, no ha-1
East Atlantic Studies
Usan Density